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Experimental evidence for conspicuous coloration as a predator deterrent in Yonahlossee salamanders (Caudata: Plethodontidae)

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Abstract. Amphibians are renowned for the variation in the colour and patterns of their integument, both within and between species. Some amphibian taxa are well known for using conspicuous coloration to signal their unpalatability to potential predators. Amphibian integument secretions contain biologically active compounds that are the source of unpalatability. Although the selective advantages are poorly understood, salamanders are often brightly coloured and secrete mucous-like substances that may serve physiological and defensive functions. In the southern Appalachians, two closely related species, the Yonahlossee salamander (*Plethodon yonahlossee)* and Northern grey-cheeked salamander (*P. montanus*), display vastly different coloration; yet, the signaling function of integument coloration is not well studied. While *P. yonahlossee* has a large red dorsal patch, *P. montanus* is uniformly grey which might indicate that there is a selective benefit of this dorsal patch. Here, we test the hypothesis that the red coloration of *P. yonahlossee* is an aposematic signal that communicates unpalatability to potential predators and predict that avian predators will avoid depredating this species. We used plasticine models of both species to experimentally test whether predators depredate conspicuously coloured models less frequently than dull models. Avian predation rates on grey models were significantly higher compared to that of red models, suggesting that the red dorsal coloration of *P. yonahlossee* is interpreted as a warning signal that deters predation. Future research should address whether *P. yonahlossee* is unpalatable or is effectively mimicking a sympatric aposematic species.

Key words. Amphibia, *Plethodon montanus*, *P. yonahlossee,* aposematism, anti-predator, integument, mimicry.

Introduction

Animals use a variety of signals to communicate with one another, including conspicuous coloration. When conspicuous coloration of potential prey is coupled with a secondary defense, such as venom or poison, colour alerts predators to the unprofitability of the prey in a phenomenon known as aposematic signaling (reviewed by Summers et al. 2015). Signals are considered honest when they accurately relay information, dishonest when they do not (Dawkins & Guilford 1991) and become established in a population when they increase individual fitness (Owren et al. 2010). Cott (1940) suggested that some colours and colour combinations (red, yellow, and white, often in combination with black) are broadly used in aposematic signaling because they increase predator recognition of signals of unpalatability. Predators either innately avoid certain conspicuous colours (Smith 1975) or learn over time to associate the colour with the defense, and thus alter their behavior to attack more profitable prey (Mappes et al. 2005).

Poison dart frogs are particularly well-known aposematic signalers. Several species of the frog family Dendrobatidae, such as the strawberry poison frog (*Oophaga pumilio*), display bright red, yellow, orange, metallic green, or blue integument coloration (Siddiqi et al. 2004), and recent field experiments using plasticine models demonstrate that predators avoid poison dart frogs with conspicuous coloration (Saporito et al. 2007). Integument secretions of some dendrobatid species contain a variety of biologically active compounds that are distasteful or harmful to most predators (Daly et al. 2005).

Other amphibians, including salamanders, also secrete mucous-like substances that may serve physiological and defensive functions (Toledo & Jared 1995). In family Salamandridae, representatives of the genera *Taricha, Notophthalmus, Cynops,* and *Titurus* secrete varying amounts of the neurotoxin tetrodotoxin (Wakely et al. 1966), and members of *Salamandra* have been found to secrete the steroidal alkaloids samandarine and samandarone which contribute to chemical defense (Mebs & Pogoda 2005, Lüddecke et al. 2018). Studies of chemical analysis of integument secretions of salamanders outside of the family Salamandridae are underrepresented in published literature, however; several studies have used behavioral trials and toxicity assays to determine level of unpalatability in the families Plethodontidae and Ambystomatidae. Representatives of both families secrete mucous-like substances when threatened, some of which seem to deter predation by vertebrates and sicken or kill them when injected into the skin (Brodie & Gibson 1969, Dodd et al. 1974, Hensel & Brodie 1976, Brandon & Huheey 1981).

In the Southern Appalachian Mountains, several species of lungless salamanders, family Plethodontidae, display conspicuous integument patterning and coloration, but the signal function of integument colour and chemical makeup of integument secretions are largely unexplored in scientific literature. To experimentally test whether one species of conspicuously coloured salamander is using integument coloration to avoid predation, potentially as an aposematic signal, we used plasticine models of two local, sympatric salamander species, one with conspicuous coloration (Yonahlossee salamander, *Plethodon yonahlossee*) and one without (Northern gray-cheeked salamander, *P. montanus*), to investigate predator response to differences in their coloration. We expected that predators would avoid the more conspicuous models, as they would associate the coloration with unpalatable integument secretions.

Materials and methods

Study species

Both *P. yonahlossee* and *P. montanus* occur sympatrically in the Blue Ridge Mountains of North Carolina, northeastern Tennessee, and southwestern Virginia (Petranka 1998). Like most *Plethodon* species, both are obligate terrestrial salamanders that occupy the same habitats. *Plethodon yonahlossee* has a dark dorsum with lateral white flecking (giving it a frosted appearance) and a large red to copper dorsal patch which extends from the base of the head to the base of the tail (Fig. 1A). Conversely, *P. montanus* exhibits a less conspicuous integument, appearing uniformly grey (Fig. 1B). The close phylogenetic relationships coupled with differences in integument coloration make these excellent species to explore the signaling function of salamander coloration.

Clay model replicas

We used pre-coloured, non-hardening, non-toxic modeling clay (Sculpey III) to make model replicas of both *P. yonahlossee* and *P. montanus* (Fig. 2). Plasticine models are useful for field experiments as they retain impressions from predation attempts and have been used successfully in previous studies of aposematic coloration and mimicry in insects, amphibians, and reptiles (Brodie 1993, Brodie & Moore 1995, Kuchta 2005, Saporito et al. 2007, Rössler et al. 2018). To make the models, we used a hardened clay mold of a formalin-fixed *P. yonahlossee* specimen that measured 15 cm total length which falls within the natural size range of adult *P. yonahlossee* (11–22 cm) and *P. montanus* (9–18.4 cm). *Plethodon yonahlossee* models were uniformly dark grey (medium gray mixed with black clays) with a large red (orange mixed with brown clays) dorsal patch extending from the base of the head to the base of the tail while *P. montanus* models were uniformly medium grey. Models were made without legs to reduce

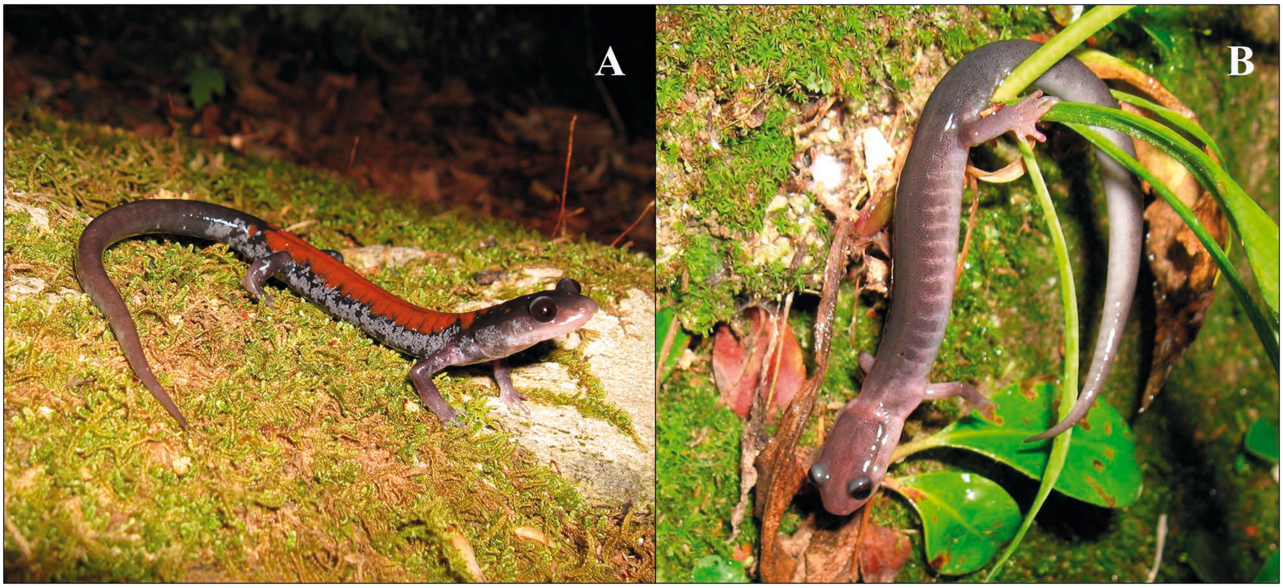

Figure 1. Life images of (A) the Yonahlossee salamander (*Plethodon yonahlossee*) and (B) Northern gray-cheeked salamander (*P. montanus*). Photos: M. Worth Pugh.

production time and also because these small structures would likely break or be degraded in transport. This gave our models a "worm-like" appearance but it is unlikely that the presence or absence of legs on models would affect a predator's decision to attack them. Moreover, live salamanders often appear "worm-like" when observed from above, so we feel that our models were similar enough to trigger a predatory response from common salamander predators (i.e., birds, small mammals).

Figure 2. Images of clay models used in experiment (*Plethodon yonahlossee*, left; *P. montanus*, right). Photo: M. Winebarger.

To select clay colours that closely matched reflectance spectra of live salamanders we measured the spectral reflectance of 60 *P. yonahlossee* and 76 *P. montanus* as well as each colour of clay and clay mixtures using an Ocean Optics S2000 spectrophotometer (range 250–880 nm: Dunedin, FL, USA) using a bifurcated micron fiber optic probe (see Steffen & McGraw 2007). The probe was maintained at a fixed distance (1 mm) and angle (90°) from the skin surface by placing the probe within a rubber stopper held flush with the salamander's skin surface. We illuminated a $2\ \mathrm{mm}^2$ measurement area with a tungsten-halogen bulb, and generated reflectance data by comparing integument reflectance to a white standard (Labsphere, Inc.). To quantify dorsal coloration, we used reflectance data to calculate red chroma and brightness. Red chroma is the measure of the proportion of light reflected in the red region, calculated as reflectance from 605–700 nm divided by the total reflectance (300–700 nm; Montgomerie 2008), so that an animal with greater red colour will have a higher value of chromatic variation in spectral reflectance. We calculated brightness, or the total amount of light reflected by the skin, as the mean of the summed reflectance from 300–700 nm; brightness can be thought of as lighter (brighter) or darker coloration (achromatic variation in spectral reflectance).

Experimental design

To assess predation under natural conditions, we surveyed Appalachian State University's Gilley Field Station (Watauga Co, NC) in May 2016, to ensure both study species occurred in the area. We then conducted three separate trials, each with 800 models: 400 *P. yonahlossee* and 400 *P. montanus*. We arranged models in a 10 × 10 model grid in eight $30\ \mathrm{m}^2$ plots, located throughout the study area. Each plot consisted of 50 models of each species (100 total), spaced at least 0.6 m between each model on all sides. Plots were separated by at least 100 m. To avoid spurious loss of models, we used black biodegradable sushi trays filled with leaf litter as foraging units. To avoid bias in model placement, we flipped a coin or rolled a die to determine which species model to place in each tray. We conducted the first trial June 16th 2016 through June 23rd 2016 (8 days), the second trial July 8th 2016 through July 11th 2016 (4 days), and the third trial September 13th 2016 through September 20th 2016 (8 days), and used new models for each trial.

Quantifying predation

We assessed each model for presence/absence of attacks and assigned each attack mark to a predator type, including only birds and mammals and disregarding those marked by invertebrates (i.e., snails). We consulted R. Wayne Van Devender (Appalachian State University Curator Emeritus of Vertebrate Collections) for guidance on determining which local predators were likely responsible for marks on models (R. W. Van Devender pers. comm.). Following the method of Saporito et al. (2007), we considered multiple marks on a single model as a single predation attempt. We quantified predation attempts by mammals for the first two trials only due to time and labor constraints. However, models appeared to have been attacked predominantly by shrews (*Blarina* and *Sorex* species) and small rodents (e.g., White-footed mouse, *Peromyscus leucopus*; Eastern grey squirrel, *Sciurus carolinensis*; Eastern chipmunk, *Tamias straitus*). These predators have poor colour vision in longer wavelengths (605–700 nm) (Vestal & Hill 1972, Jacobs and Neitz 1987, Jacobs 1993) making it unlikely that they were able to discriminate between the colours of the models. Therefore, we elected to focus on attacks by avian predators which were the most likely to respond to colour signals.

Over the course of the 3 trials, 152 models were not recovered (6.8 %) many of which were lost due to a severe storm event during the second trial. We did not include missing models in our analyses. The final sample sizes analyzed were 2,248 models (1,103 *P. montanus* and 1,145 *P. yonahlossee*) for avian predators and 1,533 models (769 for *P. montanus* and 764 for *P. yonahlossee*) for mammalian predators.

Statistical design

To determine whether salamander model colour was a significant predictor of predation, we used a generalized linear mixed model with a binomial error distribution. Generalized linear mixed models are useful for answering ecological questions when data contain variables which are non-normal and cannot be transformed (e.g. yes/no or present/absent data) and contain both fixed and random effects (Bolker et al. 2009). Because we were specifically testing the effect of model colour on predation attempts, we ran the analysis with model type as a fixed effect. To account for possible non-independence of samples within plots as well as temporal variance (trial number), we used trial and plot ID as random effects. We report residual degrees of freedom. To qualitatively assess similarity of clay models to live animal coloration, we compared the range of red chroma and brightness measures of all the live animals with the values generated from the clay models. All statistical analyses were performed using the lme4 package in R (Bates et al. 2015, R Core Team 2016).

Results

Over the course of the three trials, models were attacked largely by avian and mammalian predators (Figs 3A–C). We also observed widespread grazing on clay models by common land snails (> 50% across all models) that produced honeycomb-shaped impressions using their radulas (Fig. 3D). Across all three trials, 179 were attacked by avian predators (8.0%) and, of the models attacked by avian predators, 107 (59.8%) were *P. montanus* and 72 (40.2%) were *P. yonahlossee* (Fig. 4A). Mammalian predators attacked 437 models (28.5%) across the first two trials. Of models attacked by mammals, 235 (53.8%) were *P. montanus* and 202 (46.6%) were *P. yonahlossee* (Fig. 4B). Generalized linear mixed-effect models demonstrated that salamander model colour was a significant predictor of avian predation; grey models were depredated more often compared to red models ($z = -2.64$, $p = 0.008$, $k = 1$, 95% CI = (-0.74 to -0.11)). Conversely, colour was not a significant predictor of mammalian predation attempts ($z = -1.88$, $p = 0.06$, $k = 1$, 95% CI = (-0.34 to -0.10).

The red chroma of the clay models fell within the range of the red chroma measured from the live animals for both *P. yonahlossee* (live model range: 0.23–0.50, clay model: 0.37) and *P. montanus* (live model range: 0.09–0.29, clay model: 0.27) (Fig. 5). However, the clay models were brighter than the live models (*P. yonahlossee* live model range: 0.01–0.11, clay model: 0.20; *P. montanus* live model range: 0.004–0.15, clay model: 0.21).

Discussion

We found that avian predators were more likely to attack uniformly grey models than models with a large red dorsal patch. Moreover, although they attacked red models less, mammalian predators did not discriminate among colour morphs significantly. This is despite the fact that they attacked more models across two trials than avian predators did among three. These results are consistent with the hypothesis that the red dorsal patch of *P. yonahlossee* acts as an aposematic signal to potential predators with particular regard to those that locate their prey visually. The plots were designed to be analogous to a choice test such that predators would be able to view the two different models simultaneously and choose which to attack. Although the data support the hypothesis that the red patch is an aposematic signal, because of the lack of available data on unpalatability in salamanders, it is difficult to determine whether predators avoided models with the red patch because *P. yonahlossee* is unpalatable, because predators have an innate wariness of certain colours or because *P. yonahlossee* may be similar in coloration to an aposematic species (mimicry). Nonetheless, the red coloration is likely interpreted by predators as a warning signal that deters predation.

One plausible explanation of this trend is that the function of *P. yonahlossee* dorsal coloration is to mimic poisonous Eastern newts (*Notophthalmus viridescens*). *Notophthalmus viridescens* skin secretions contain tetrodotoxin (a potent neurotoxin) used as a defense against predators and this species occurs sympatrically with *P. yonahlossee* throughout its range (Petranka 1998). During its intermediate terrestrial stage of development (red eft stage) *N. viridescens* displays a brilliant orange-red colour which is thought to signal unpalatability to predators (Mitch-

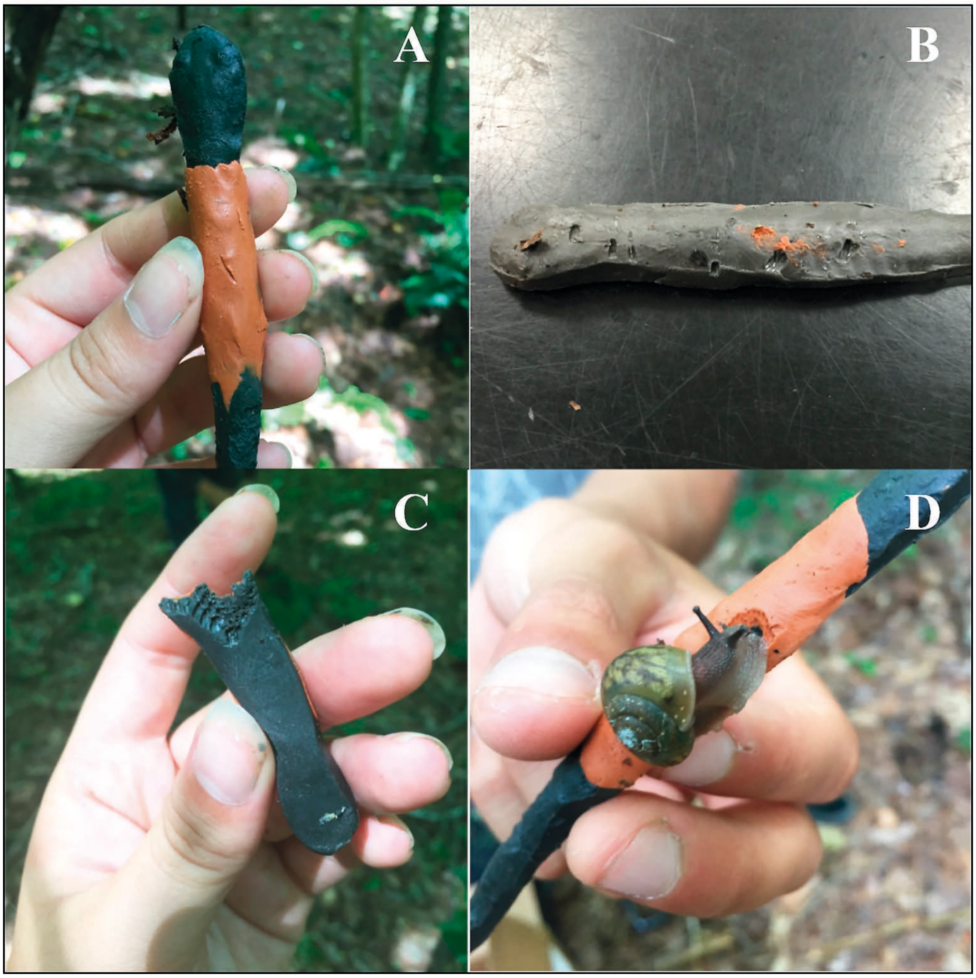

Figure 3. Images of (A) avian, (B–C) mammalian, and (D) snail markings on clay models. Photos: M. Winebarger.

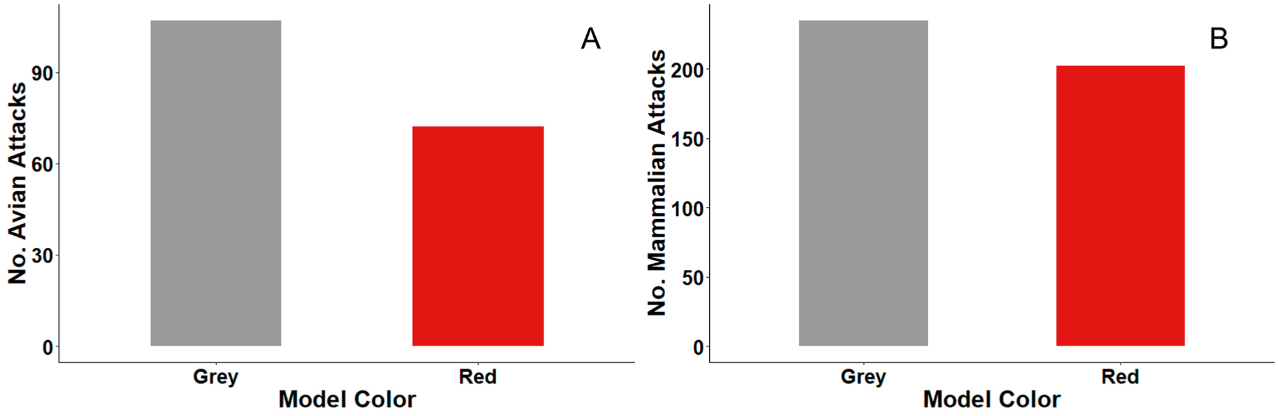

Figure 4. Total number of predation attempts on grey and red salamander models by (A) avian and (B) mammalian predators.

ell & Gibbons 2010). Additionally, Caspers et al. (2020) found that predators avoid clay models with yellow coloration to mimic poisonous fire salamanders (*Salamandra salamandra*) suggesting local predators avoid prey items that resemble toxic salamanders. Many other salamanders with red coloration occur sympatrically with *N. viridescens*, and these geographical associations have been used as an argument in support of Batesian mimicry of the toxic species (Brodie 1977). However, *P. yonahlossee* may be unpalatable or even toxic. Some predominantly red species of plethodontid salamanders, such as *Pseudotriton ruber* and *Pseudotriton montanus*, secrete toxic compounds that can induce death of chickens and mice (Brandon & Huheey 1981). Further, *Plethodon jordani*, which typically has red patches on its cheeks, has also been found to be unpalatable to some predators in behavioral trials (Brodie & Howard 1973, Hensel & Brodie 1976). Although the toxicity of *P. yonahlossee* has yet to be tested, the unpalatability of other plethodontids suggests *P. yonahlossee* is signaling warning coloration or is a Mullerian mimic. Most plethodontid salamanders, including both *P. yonahlossee* and *P. montanus*, are nocturnal species and are primarily active on rainy nights (Petranka 1998), thus; evolving conspicuous signals to potential predators may seem counterintuitive. However, *Plethodon* species are often active in the leaf litter on days with cloud cover and can be found under cover objects on most days (Brandon & Huheey 1975). While *P. yonahlossee* is not often seen during the day, some potential predators (such as ground-dwelling songbirds, grouse, and turkeys) scratch in the leaf litter and can uncover individuals (Winebarger, pers. obs.). Moreover, despite nocturnal activity patterns, *P. yonahlossee* could have evolved warning coloration through selective pressure caused by being uncovered during the day or from nocturnal predators like owls. Indeed, within the caecilian clade (Amphibia: Gymnophiona), which contains representatives that are typically fossorial, species slightly more prone to surface activity have also evolved conspicuous contrasting patterns and yellow integument pigmentation (Wollenberg & Measey 2009). Thus, there are several plausible explanations for avian predators avoiding models that resemble *P. yonahlossee*.

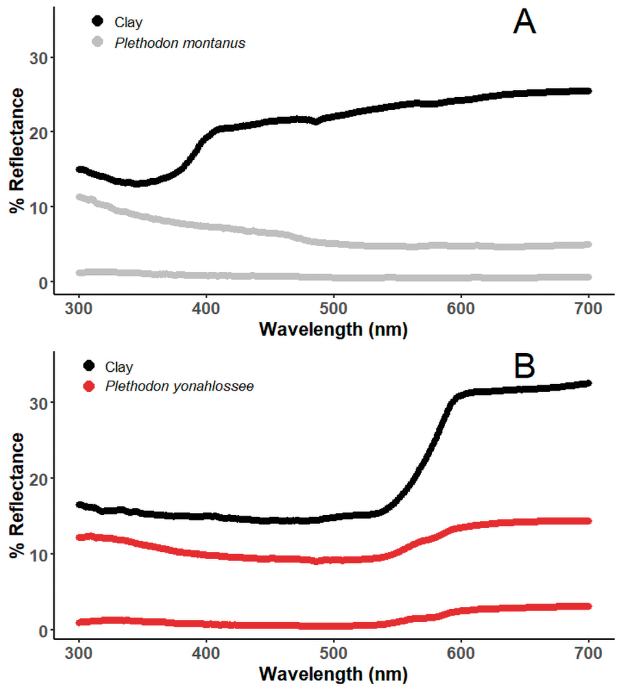

Figure 5. Reflectance spectra of clay color vs live salamander colour (most and least bright individuals) for (A) *Plethodon montanus* and (B) *P. yonahlossee*.

The red-orange and grey clay models were good chromatic matches as the red chroma fell well within the natural range of red chroma of each respective live species. However, for both species, the clay models were brighter (expressed greater achromatic coloration) compared to the live animals. Our goal was to match the chromatic variation as the colour of two species differ mainly in chroma (spectral shape) rather than brightness (achromatic colour aspects measured as overall area under the curve). Moreover, because the clay models of both species were brighter (~15% brighter) than their live counterparts, and because the experimental design was set up as a choice test, we think it is unlikely that greater brightness of the clay models influenced predator choice. To our knowledge, this is the only study to compare reflectance spectra of models and live animals across all wavelengths visible to birds (300–700 nm).

These data suggest that avian predators avoid the conspicuously coloured model salamanders and, while our study does not rule out the possibility of mimicry, no studies have rigorously tested whether *P. yonahlossee* is a mimic of *Notophthalmus viridescens*. Further, *Plethodon* species have large granular glands in their integument and future research should focus on identification and quantification of potentially noxious compounds derived from *Plethodon* integument. This information is critical to understanding coloration and anti-predator systems in *Plethodon* as well as signaling function in other amphibian clades. Subsequent studies should investigate the palatability of plethodontids to common salamander predators as well as biochemical properties of slime secretions. Such investigations could reveal evolutionary mechanisms behind the often brilliant colours displayed by these diminutive vertebrates.

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